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DIFFERENTIATION OF SYMPATHETIC NEURONES PROJECTING IN THE HYPOGASTRIC NERVES IN TERMS OF THEIR DISCHARGE PATTERNS IN CATS

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SUMMARY

1. Sympathetic neurones that project in the hypograstric nerves (HGNs) were analysed for their discharge patterns in anaesthetized cats. The activity of these neurones was recorded from their axons. Afferents from the pelvic organs (urinary bladder, colon, anal canal), and arterial baro- and chemoreceptors were stimulated. 150 postganglionic and nine preganglionic neurones were analysed.

2. The postganglionic neurones exhibited reflex patterns that were typical of visceral vasoconstrictor neurones and various types of motility-regulating neurones. Most motility-regulating neurones and all visceral vasoconstrictor neurones had ongoing activity.

3. Postganglionic motility-regulating neurones were not influenced by stimulation of arterial baro- and chemoreceptors, but showed distinctive reflexes on stimulation of afferents from pelvic organs. Three subgroups of motility-regulating neurones were identified: type 1 neurones (34% of the sample of postganglionic neurones) were excited from the urinary bladder and inhibited or not influenced from the colon. Type 2 neurones (14%) exhibited a reflex pattern reciprocal to that of the type 1 neurones. Anal motility-regulating neurones (8%) were only influenced from the anal canal. The most powerful reflexes in these types of motility-regulating neurones were elicited by mechanical stimulation of the anal mucosa.

4. Postganglionic visceral vasoconstrictor neurones (16% of the sample) were under powerful inhibitory control from the arterial baroreceptors and weakly excited by stimulation of arterial chemoreceptors. Visceral stimuli had little or no effect on most of these neurones. Some visceral vasoconstrictor neurones exhibited some overlap in their functional properties with motility-regulating neurones.

5. Twenty-eight per cent of our sample of postganglionic neurones showed no

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reflexes to the afferent stimuli used. About half of these neurones had on-going activity.

6. Nine preganglionic neurones with on-going activity were identified. Most of these neurones behaved like visceral vasoconstrictor or motility-regulating neurones.

7. This study shows that the majority of postganglionic neurones that project in the HGNs can be divided into the same functional types as the lumbar preganglionic neurones that project to the inferior mesenteric ganglion. The proportions of the different types of neurones are similar at pre- and postganglionic levels. Thus the centrally generated patterns of activity are most likely faithfully transmitted from the spinal cord to the target organs in the pelvic cavity in functionally separate pathways.

INTRODUCTION

Most preganglionic neurones of the lumbar sympathetic outflow of the cat either project in the lumbar sympathetic trunks distal to the ganglion L5 or in the lumbar splanchnic nerves. The neurones that project in the lumbar sympathetic trunk synapse with postganglionic neurones, many of which innervate target organs in skin and deep somatic tissues of the hindquarters (Jänig, 1985, 1986, 1988) and some of them innervate the pelvic organs (Langley & Anderson, 1895*a*; Kuo, Hisamitsu & de Groat, 1984). The neurones that project in the lumbar splanchnic nerves synapse either with postganglionic neurones in the inferior mesenteric ganglion (IMG) or in some corresponding intercalated smaller ganglia and/or, after projecting further via the hypogastric nerves (HGNs), with postganglionic neurones in the pelvic ganglia (Baron, Jänig & McLachlan, 1986*a*). Most neurones in the rostral lobes of the IMG project to the colon (Julé & Szurszewski, 1983; Baron, Jänig & McLachlan, 1986*b*) and are involved in regulation of motility and secretory processes as well as vasculature of the colon. Most neurones in the caudal lobes of the IMG project to the pelvic organs (Julé & Szurszewski, 1983; Baron *et al.* 1986*a*). These neurones are involved in the regulation of the lower urinary tract, distal hindgut, internal reproductive organs and the vasculature of these organs (Langley & Anderson, 1895*a*, *b*, *c*; for review see Jänig & McLachlan, 1987).

Sympathetic preganglionic neurones that project in the lumbar splanchnic nerves have been functionally classified into several subgroups using neurophysiological methods and natural stimulation of sensory receptors (Bahr, Bartel, Blumberg & Jänig, 1986*a*, *b*, *c*). The majority of the neurones are not influenced by stimulation of arterial baroreceptors and chemoreceptors and their activity is not related to the central regulation of the respiratory system. Rather, these neurones exhibit powerful excitatory and inhibitory reflexes when visceral sacral afferent neurones from the pelvic organs (urinary bladder, colon, anal canal) are stimulated. They are probably not involved in the regulation of the vasculature but in the regulation of motility and secretory processes of the evacuative organs. We have called these neurones 'motility-regulating' neurones. They consist of several subtypes.

A second group of preganglionic neurones is under powerful inhibitory control by arterial baroreceptors, excited by stimulation of arterial chemoreceptors and centrally coupled to the regulation of respiration (Bahr *et al.* 1986*b*; Boczek-Funcke, Häbler, Jänig & Michaelis, 1989). These neurones exhibit no or only weak excitatory

reflexes on stimulation of sacral visceral afferent neurones. They are probably involved in regulation of resistance of the visceral vascular bed. We have called these neurones 'visceral vasoconstrictor' neurones. There is a small amount of overlap in the reflex responses between the preganglionic motility-regulating and visceral vasoconstrictor neurones.

A third group of preganglionic neurones is almost silent and discloses inconsistent or no reflexes when adequate stimuli are applied to the pelvic organs or the perineal skin. Some of these neurones may be involved in activation of the internal reproductive organs.

In the present investigation we focused on the questions, first, whether the neurones that project in the hypogastric nerves can also be subclassified functionally by way of their reflex patterns and, secondly, what are the relative sizes of these different classes of neurones? This second point should be seen in the context of the general question of whether the quite different centrally generated discharge patterns in the preganglionic visceral vasoconstrictor and motility-regulating neurones also occur in the postganglionic neurones and are therefore transmitted in separate peripheral pathways to the target organs of the visceral sympathetic outflow. The present experimental investigation fully supports this contention. Some results have been published in preliminary form (Jänig, Schmidt, Schnitzler & Wesselmann, 1987).

METHODS

Anaesthesia and animal maintenance

Thirty-six adults cats of either sex weighing 2·2–4·5 kg were used. Following induction with ketamine (Ketanest®; 15–20 mg kg^{-1}, I.M.) the animals were anaesthetized with α-D-gluco-chloralose (50 mg kg^{-1}, I.P.). Supplementary doses of 5–10 mg kg^{-1} α-D-gluco-chloralose were given intravenously to maintain deep anaesthesia as judged by the persistence of miotic pupils and the lack of heart rate and blood pressure fluctuations in the absence of visceral stimuli. Blood pressure and heart rate were continuously recorded after cannulation of the common carotid artery and the mean arterial pressure was always 100 mmHg or higher. Drugs were injected into the external jugular vein. Animals were paralysed by pancuronium bromide (Pancuronium^{R}; 0·2 mg kg^{-1} per bolus, total dose as required, I.V.) and artificially ventilated through a tracheal cannula, keeping the end-expiratory CO_2 concentration at about 4%. Body core temperature was measured intraoesophageally and maintained close to 38 °C. The urinary bladder was catheterized via the urethra in order to measure the volume of excreted urine for proper control of fluid balance. The experiments usually lasted for 20–24 h at the end of which the animals were killed by intravenous injection of a saturated potassium chloride solution or by I.V. injection of an overdose of pentobarbitone.

Nerve preparations

Most sympathetic preganglionic neurones that project in the hypogastric nerves (HGNs) are situated in the spinal segments L3 and L4 with a maximum in L4 (Baron, Jänig & McLachlan, 1986*c*). The lumbar sympathetic trunk from ganglia L2–L5, the lumbar white rami L3 and L4, the lumbar splanchnic nerves, the inferior mesenteric ganglion (IMG) and both HGNs were exposed on the left side using a lateral retroperitoneal approach. For this purpose, the lateral processes of the vertebra were removed. The white rami were dissected free for 8–10 mm and isolated from the surrounding tissue by small pieces of parafilm sheet. The white ramus L5 was cut if present (see Baron, Jänig & McLachlan, 1985). The lumbar sympathetic trunk was cut rostrally to the ganglion L3. The right lumbar ganglia L2–L5 of the sympathetic trunk were removed, eliminating in this way a large part of the preganglionic input to the HGNs and possibly also to postganglionic neurones that project in the right HGN (Baron, Jänig & McLachlan, 1986*a*) in order to increase the chance of obtaining single postganglionic units with reflex and on-going activity from the right

HGN which receives the remaining preganglionic input from the left side. The white rami were put on pairs of platinum electrodes for electrical stimulation. The HGNs were dissected free for about 10 mm at a point 15–20 mm distal to the IMG. Both hypogastric nerves were put on a rigidly fixed black Perspex plate.

The inferior mesenteric artery was ligated near its division into the arcade arteries. A thin catheter was inserted into the artery central to the ligation with its tip positioned close to the IMG. This procedure did not lead to ischaemia of the colon because the rostral and caudal blood supplies of this organ were preserved (see Blumberg, Haupt, Jänig & Kohler, 1983). Hexamethonium was injected through this catheter in boluses of 1 ml saline containing 3 mg hexamethonium in order to temporarily block the synaptic impulse transmission in the IMG.

Neurophysiological recording and stimulation

Bundles with as few active axons as possible were isolated from the HGN on the black Perspex plate under a stereomicroscope. The activity in these bundles was recorded monopolarly using a platinum wire electrode attached to the nearby tissue as reference. Signals were amplified by low-noise differential AC amplifiers (input impedance 10 kΩ) and filtered with a variable bandwidth ranging from 20–50 Hz to 1·2–1·5 kHz. Neural activity was displayed on the oscilloscope and stored on magnetic tape for off-line analysis. After passing through a window discriminator to identify the signals of single units, the neural activity was read into a laboratory computer (Minc PDP 11) to construct peristimulus histograms. The axons in the bundles were identified as postganglionic and preganglionic or afferent as described in the first part of the Results.

Stimulation of afferents

Arterial baroreceptors. Stimulation of arterial baroreceptors leads to inhibition of activity in vasoconstrictor neurones innervating resistance vessels. Possible vasoconstrictor units were identified in two ways:

(1) Cardiac rhythmicity of the activity in the sympathetic neurones was determined by correlation of unit discharge with the R-wave of the ECG (recorded differentially from both forepaws or from one forepaw and the left upper thoracic wall). The activity in the sympathetic neurones was sampled over 50–1000 time periods of two cardiac cycles at a bin width of 8 ms with a multichannel counter (Didac 800 from Intertechnique). The 'degree of cardiac rhythmicity' in the neuronal activity (percentage difference between the minimum and maximum of the activity in the superimposed histogram) is a measure of inhibition caused by phasic activation of the arterial baroreceptors (Blumberg, Jänig, Rieckmann & Szulczyk, 1980).

(2) The arterial baroreceptors were stimulated by increasing the arterial blood pressure by I.V. injections of adrenaline or noradrenaline (0·5–1·5 μg (kg body weight)$^{-1}$). Using this method, only the inhibition of postganglionic activity that occurs immediately with the increase of the arterial blood pressure is a positive sign for reflex inhibition because catecholamines depress the synaptic transmission in the sympathetic ganglia (Jänig, Krauspe & Wiedersatz, 1982). Depression of activity in peripheral ganglia produced by the action of the injected catecholamines is delayed and not as abrupt since they reach the IMG after about 10 s.

Arterial chemoreceptors. Arterial chemoreceptors were stimulated in two ways:

(1) A thin catheter was inserted into the left lingual artery with its tip close to the carotid glomus. Injections of small boluses of about 0·2–0·5 ml of CO_2-enriched saline solution through this catheter stimulated the arterial chemoreceptors (twenty experiments; see Blumberg *et al.* 1980).

(2) The animals were respired with a hypoxic gas mixture of 8% O_2 in N_2 for 1·5–3 min (see Blumberg *et al.* 1980).

Afferents from the pelvic organs. The afferents innervating the urinary bladder were stimulated in two ways:

(1) Fluid was injected in volumes of 5–10 ml through the urethral catheter so as to distend the organ passively.

(2) The organ was induced to contract isovolumetrically at intravesical volumes of about 20–40 ml saline. The intravesical pressure was measured by a pressure transducer that was connected to the urethral catheter. Both procedures selectively excite spinal and lumbar afferents from the urinary bladder (Bahns, Ernsberger, Jänig & Nelke, 1986; Bahns, Halsband & Jänig, 1987).

A thin-walled latex balloon of 10–15 cm length was inserted transanally into the colon so that the distal end of the balloon was positioned 1–2 cm rostral to the anal canal. The ballon was mounted around a flexible tube (inner diameter 5 mm) through which it was filled with water at room temperature. Twenty to 80 ml fluid was injected manually using a syringe. The intracolonic pressure that developed passively or during the contractions of the colon was measured by a pressure transducer that was connected to the flexible tube. This procedure stimulates afferents from the colon but not afferents from the anal canal, with some occasional discharges in the latter ones at the beginning and the end of a distension of the colon (Bahns *et al.* 1987; Jänig & Koltzenburg, 1991).

Receptors in the mucosal skin of the anal canal were stimulated mechanically by rostro-caudal shearing stimuli. This stimulus excites afferents from the anal mucosa but not ones from the colon (Bahns *et al.* 1987; Jänig & Koltzenburg, 1991). Perigenital hairy skin (that included the perineal skin between testes or vagina and anal canal) was stimulated mechanically with a spatula; care was taken that anal skin was not stimulated during this procedure. Afferents from the urethra were stimulated by small movements of the urethral catheter (tapping, pulling, lateral movements; see Bahns *et al.* 1986, 1987).

Data acquisition and analysis

Intravesical and intracolonic pressure recordings, blood pressure recordings and neural activity were stored on magnetic tape (SE 7000, EMi) for off-line analysis with a laboratory computer. Some data were displayed on the oscilloscope for photography.

RESULTS

The results described in this paper were obtained from 150 postganglionic neurones and nine preganglionic neurones that projected in one of the hypogastric nerves (HGN). Results obtained from multi-unit bundles that were isolated from the hypogastric nerves are not included in this paper.

We functionally classified the neurones in the same way as described recently for the lumbar preganglionic neurones that project in the lumbar splanchnic nerves (Bahr *et al.* 1986*a*, *b*). According to these studies the postganglionic neurones were *a priori* divided into the following functional groups: motility-regulating type 1 neurones, motility-regulating type 2 neurones, neurones only influenced from the anal canal and visceral vasoconstrictor neurones. Functional characteristics and other properties of these neurones are listed in Table 1.

Identification of neurones projecting in the hypogastric nerves

In the cat, approximately 20000 neurones project in one HGN, about 17000 being postganglionic (15000 of them having their cell bodies in the inferior mesenteric ganglion (IMG) and the rest in intercalated ganglia, the intermesenteric nerve and paravertebral ganglia), about 1300 preganglionic and 1700 afferent. The cell bodies of about 20% of the preganglionic and afferent axons are located on the contralateral site in the dorsal root ganglia and in the spinal cord (Baron *et al.* 1986*a*, *c*). Only very few sacral afferent, and sacral preganglionic and postganglionic neurones project from the pelvic cavity through the HGN to the IMG (Baron & Jänig, 1988).

The locations of cell bodies and types of neurones that project in the HGNs are illustrated in Fig. 1. We recorded from the central ends of axon bundles that were isolated from one of the HGNs about 15–20 mm distal to the IMG (arrow in Fig. 1). As predicted by the quantitative morphological data, the cases *c* and *d* (Fig. 1) were

the most common ones and the cases *a* and *b* much less frequent. It was difficult to isolate and recognize single preganglionic axons (case *e* in Fig. 1).

Figure 2 illustrates the identification of neurones that project in bundles isolated from the HGN. The bundle in *A* contained two units that were activated from the

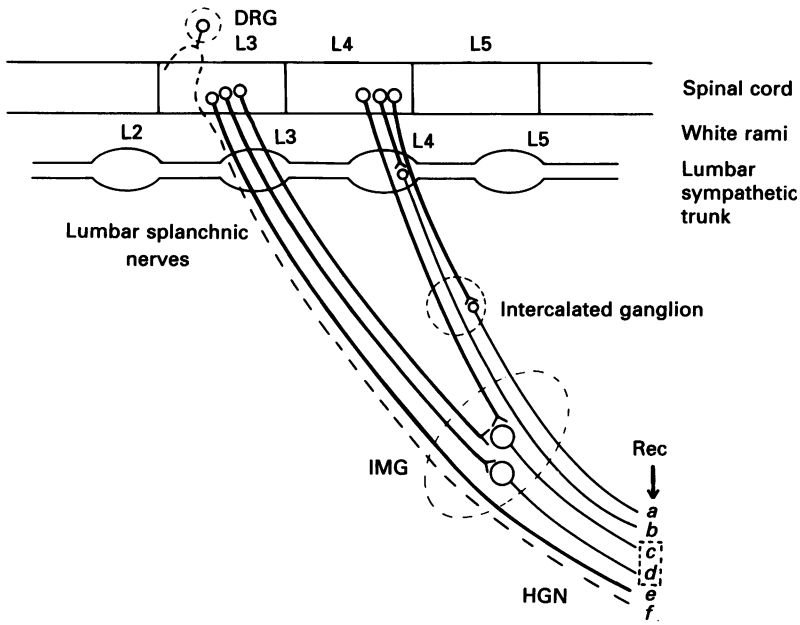

Fig. 1. Types of neurones projecting in the hypogastric nerves (HGNs) that are activated on electrical stimulation of the white rami L3 and L4 and the position of the cell bodies of these neurones. Cases *c* and *d* are the most common ones (postganglionic, cell bodies in the IMG); the activity in these neurones can readily be blocked by hexamethonium applied locally to the inferior mesenteric ganglion (IMG). Neurones of type *e* (preganglionic) and *f* (afferent) show constant latencies and follow repetitive electrical stimulation of the white rami at high frequency. Neurones of type *a* and *b* are rare (postganglionic, cell bodies in intermediate or paravertebral ganglion).

white rami. Unit 1 was postganglionic: it had on-going activity (upper trace in Fig. 2*A*) and was activated by electrical stimulation of the white ramus L3 or L4 with single supramaximal impulses (case *c* in Fig. 1). The responses showed some scatter in their latencies consistent with the synaptic transmission in the IMG. Unit 2 was only activated by electrical stimulation of the white ramus L3, at constant invariant latency. It had no resting activity and showed no reflexes. It was therefore either an afferent axon or the axon of a silent preganglionic neurone (see *e* and *f* in Fig. 1).

Figure 2*B* illustrates the identification of three postganglionic neurones with on-going activity before and after an injection of a bolus of hexamethonium solution into the arterial circulation of the IMG (see Methods). Units 3 and 4 were activated by electrical stimulation of the white ramus L3 (second trace in Fig. 2*B*) but not from the white ramus L4; unit 5 could neither be activated from white ramus L3 nor from white ramus L4. Hexamethonium blocked the on-going activity as well as the evoked

activity in the units (lower trace in Fig. 2*B*). The block occurred immediately in units 3 and 4 and was delayed for about 20 s in unit 5. Thus units 3 and 4 presumably had their cell bodies in the IMG, but unit 5 did not.

Postganglionic type 1 motility-regulating neurones

A large proportion of the preganglionic neurones that project in the lumbar splanchnic nerves are not under reflex control of the arterial baro- and chemo-

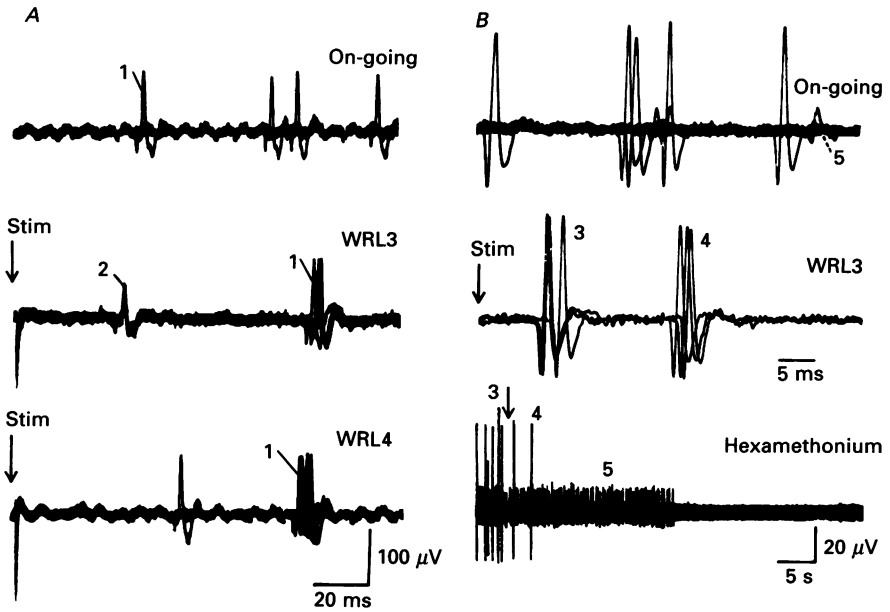

Fig. 2. Identification of single units in strands isolated from the HGN. *A*, strand with two units. Electrical stimulation of the white rami (WR) L3 and L4 with single pulses (5 V, 0·2 ms pulse duration). Unit 1 was postganglionic and unit 2 either preganglionic or afferent. *B*, strand with three postganglionic units with on-going activity (upper trace). Units 3 and 4 were activated from the white ramus L3 (10 V, 0·2 ms pulse duration). Unit 5 could not be activated from white rami L3 and L4. The on-going activity in all three units was blocked by hexamethonium (3 mg injected through the inferior mesenteric artery close to the IMG; lower trace).

receptors and exhibit distinct reflexes on adequate stimulation of sacral visceral afferents from pelvic visceral organs. We call these neurones motility-regulating neurones because they may be involved in the regulation of motility of pelvic organs (Bahr *et al.* 1986*a*; Bartel, Blumberg & Jänig, 1986). A frequently encountered type of preganglionic motility-regulating neurone is excited from the urinary bladder and either inhibited or not influenced from the colon.

In the population of postganglionic neurones that project in the HGNs, the type 1 motility-regulating neurone has a high representation. Figures 3 and 4 illustrate experiments on two postganglionic type 1 motility-regulating neurones. Neurone 1 in Fig. 3 was inhibited on distension of the colon (*A*) and excited on isovolumetric

contraction of the urinary bladder. A second neurone (neurone 2) with very low rate of on-going activity was weakly activated during contraction of the urinary bladder. Type 1 motility-regulating neurones were always excited by both passive distension of the organs and by organ contractions. Many type 1 neurones were excited by

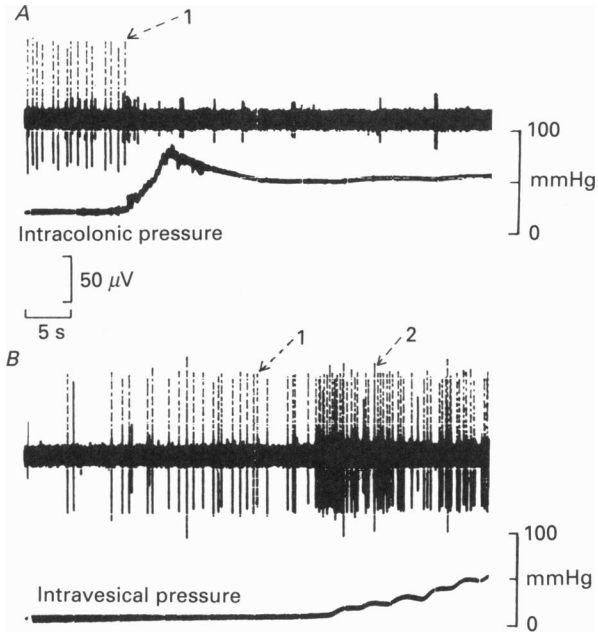

Fig. 3. Postganglionic neurone (neurone 1) with a reflex pattern of a preganglionic motility-regulating type 1 neurone. The neurone was inhibited in its activity on isovolumetric contraction of the colon (*A*) and excited on isovolumetric contraction of the urinary bladder (*B*). A second neurone (neurone 2) that barely showed any on-going activity was weakly excited during contraction of the urinary bladder. The flexible balloon in the colon contained about 50 ml water; the urinary bladder contained about 30 ml saline.

mechanical stimulation of the mucosa of the anal canal (Fig. 4*A*), and of afferents from the perigenital skin (Fig. 4*B*) and from the urethra (Fig. 4*C*). Some type 1 neurones were inhibited by mechanical stimulation of the anal mucosa and of the perigenital skin. The responses to stimulation of urethral receptors and of the urinary bladder by distension were qualitatively always identical.

About 34% of all postganglionic neurones that were analysed in this study (fifty-one out of 150 neurones) were classified as type 1 motility-regulating neurones.

Postganglionic type 2 motility-regulating neurones

Preganglionic type 2 motility-regulating neurones that project to the IMG are inhibited by stimulation of sacral vesical afferents and excited or not influenced by stimulation of sacral afferents from the colon (Bahr *et al.* 1986*a*). Figure 5 illustrates an experiment in which two postganglionic type 2 neurones were excited during contraction of the colon (Fig. 5*A*, left) and inhibited during isovolumetric contraction

of the urinary bladder. These inhibitions are clearly visible when the activity in the neurones is superimposed several times with respect to the increase of the intravesical pressure (Fig. 5*B*). Neurone 1 was weakly excited on mechanical stimulation of the anal mucosa and neurone 2 was not influenced by this stimulus. Fourteen per cent

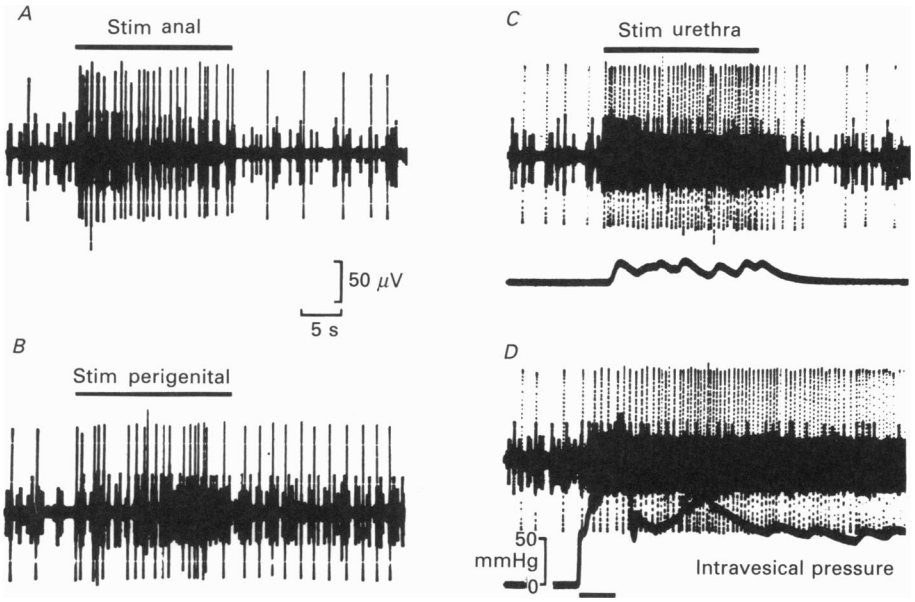

Fig. 4. Postganglionic neurones with on-going activity (large signal) excited during increase of intravesical pressure (*D*, produced by injection of 15 ml saline), on stimulation of afferents from the anal mucosa by mechanical shearing stimuli (*A*), on mechanical stimulation of perigenital skin (*B*), and on stimulation of urethral receptors (*C*, by slight disto-proximal movements of the urethral catheter). The response in *C* was as strong as that in *D* and therefore largely initiated by activity in urethral afferents and only to a small extend by activity in vesical afferents (excited by the small contractions of the urinary bladder). Note after-discharges in *A* and *B*, but their absence in *C*. This neurone was classified as a postganglionic motility-regulating type 1 neurone. Note that other neurones with similar reflex properties projected in the bundle from which the recording was made.

of postganglionic neurones (twenty-one out of 150 neurones) showed these patterns of reflex activity, and hence were classed as type 2 motility-regulating neurones. Neurones that were inhibited or excited from both the urinary bladder and the colon were not found.

Postganglion neurones responding to anal and perigenital stimulation

Mechanical stimulation of the mucosal skin of the anal canal by proximo-distal shearing movements elicited the largest excitatory reflexes in the visceral sympathetic neurones. Figure 6 illustrates an extreme case. This neurone displayed almost no on-going activity before the first mechanical stimulus was applied to the anal mucosa. A series of three episodes of mechanical stimulation at 3 min intervals,

each lasting 20 s, activated the neurone with after-discharges lasting for more than 40 min. Some postganglionic neurones are inhibited in their activity on mechanical stimulation of the receptors of the anal canal.

Sixty-six per cent of type 1 and 2 motility-regulating neurones (fifty-two out of seventy-eight neurones tested) were activated from the anal canal (see Fig. 4*A* and

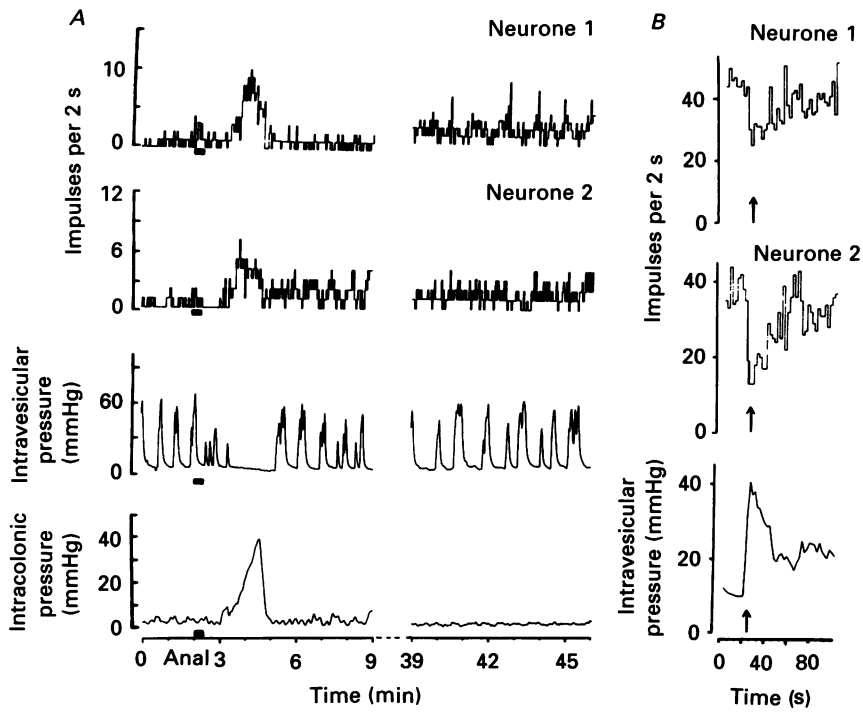

Fig. 5. Discharges of two postganglionic neurones showing patterns of reflex activity typical of preganglionic motility-regulating type 2 neurones. Both neurones were excited during contraction of the colon (left in *A*), and inhibited during isovolumetric contractions of the urinary bladder (right in *A*). Neurone 1 was weakly excited by mechanical stimulation of the anal canal and neurone 2 was not influenced (left in *A*). In *B* the activity of both neurones is 20 times superimposed with respect to the intravesical peak pressure produced by the contractions of the urinary bladder.

neurone 1 in Fig. 5*A*) and 6·5% (five out of seventy-eight neurones tested) were inhibited. The rest of the neurones were not influenced from the anal canal (see neurone 2 in Fig. 5*A*). Twelve of 150 neurones investigated (8%) were activated only from the anal canal, but showed no reflexes on stimulation of afferents from the urinary bladder and the colon. We called these neurones anal motility-regulating neurones and the neurone in Fig. 6 belongs to this group.

The discharge rate of motility-regulating neurones increased from $0{\cdot}8 \pm 0{\cdot}5$ impulses s^{-1} before stimulation to a maximum of $2{\cdot}7 \pm 1{\cdot}5$ impulses s^{-1} during mechanical stimulation of the anal mucosa (mean $\pm$ S.D., $n = 22$). Thirty-three per cent (twenty-four of forty-nine neurones tested) exhibited after-discharges, lasting for 1–15 min ($6{\cdot}9 \pm 4{\cdot}4$ min, mean $\pm$ S.D.; see Fig. 4*A*, Fig. 6).

Forty-three postganglionic neurones were tested for their responses to mechanical stimulation of both the anal canal and the perigenital skin. Eighteen neurones (42%) were either excited (see Fig. 4*A* and *B*) or not influenced by both stimuli. Twenty-five neurones exhibited differential responses: fourteen neurones (33%) were excited

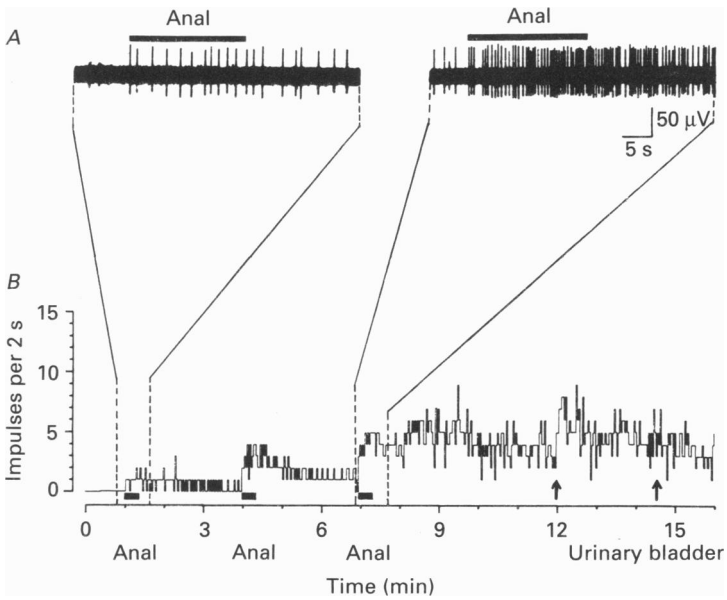

Fig. 6. Postganglionic neurone responding to mechanical shearing stimuli applied to the mucosa of the anal canal. The neurone had almost no on-going activity before the first stimulus. It responded only to anal stimuli and not to other stimuli applied to the urinary bladder (*B*), urethra and perigenital skin. Note the long-lasting enhancement of the activity after the anal stimuli.

from the anal canal and not influenced from the perigenital skin, one neurone was inhibited from the anal canal and not influenced from the perigenital skin and ten neurones (23%) were excited or inhibited from the perigenital skin and exhibited either the opposite responses from the anal canal or no responses.

Postganglionic visceral vasoconstrictor neurones

About 16% of the postganglionic neurones investigated (24 of 150 neurones tested) had functional properties typical of visceral vasoconstrictor neurones (see Bahr *et al.* 1986*b*). A typical example is illustrated in Fig. 7. These neurones were inhibited in their activity on increase of the arterial blood pressure (Fig. 7*C* and *D*) and always exhibited pronounced cardiac rhythmicity in their discharges (Fig. 7*A*). They were weakly excited on stimulation of arterial chemoreceptors, either by injection of small boluses of CO_2-enriched saline solution through the lingual artery (Fig. 7*B*) or by ventilating the animal with a hypoxic gas mixture (Fig. 7*D*). Most of them ($n = 20$) exhibited weak or no responses to stimuli applied to the pelvic organs. Four postganglionic neurones with patterns of visceral vasoconstrictor neurones (3% of the postganglionic neurones investigated) appeared to have some reflex properties of

motility-regulating neurones. They exhibited reflexes to innocuous stimulation of either the urinary bladder, the anal canal or the colon. We cannot exclude whether this was an artifact due to inadequate discrimination of signals from different axons generating signals of similar size and shape.

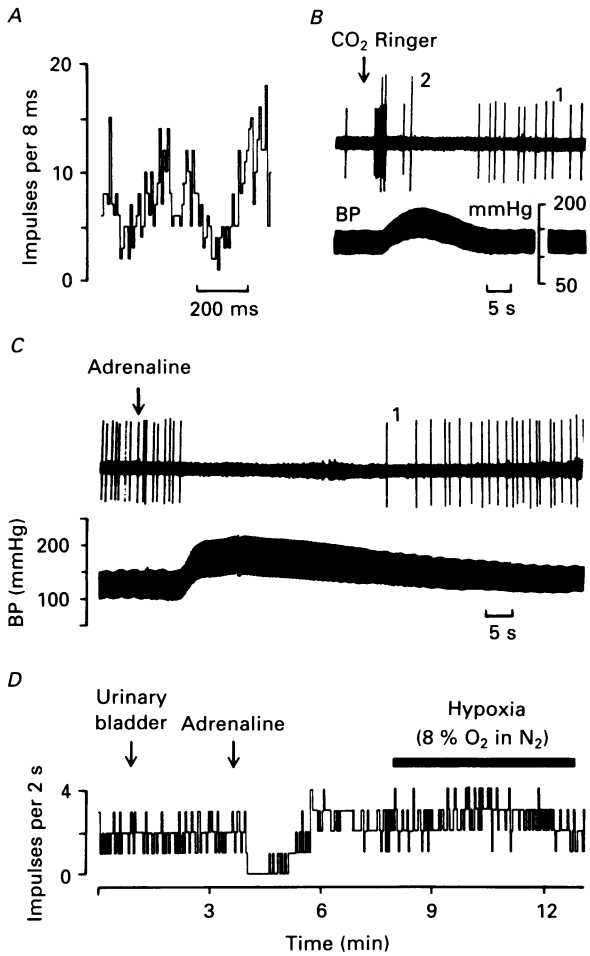

Fig. 7. Reflex patterns of a visceral vasoconstrictor neurone (neurone 1). *A*, cardiac rhythmicity of the activity. Post-R-wave histogram of a time period of two cardiac cycles obtained from 500 repetitions at a bin width of 8 ms. *B*, stimulation of the arterial chemoreceptors in the left carotid glomus by an injection of a 0·5 ml bolus of CO_2-enriched saline solution. Note that a silent neurone (2) was additionally activated. *C*, response to increase of arterial blood pressure (BP) induced by an I.V. bolus injection of 1·5 $\mu g\ kg^{-1}$ adrenaline. Note the abrupt inhibition on increase of the blood pressure. *D*, inhibitory response to I.V. injection of adrenaline (same as in *C*), weak excitation on systemic hypoxia (ventilation of the animal with a gas mixture of 8% O_2 in N_2, filled bar) and absence of responses to distension of the urinary bladder. The neurone did furthermore not exhibit reflex responses to anal, perigenital and colonic stimulation.

Non-classified postganglionic neurones

Twenty-eight per cent of the postganglionic neurones (forty-two out of 150 neurones tested) could not be classified into one of the types described above. Half of these neurones exhibited resting activity. This activity did not have any

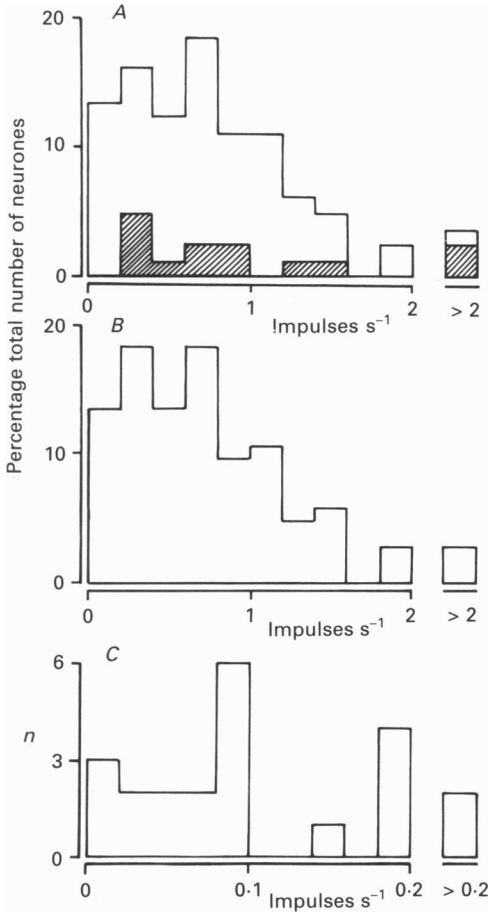

Fig. 8. Frequency distribution of on-going activity in postganglionic neurones. *A*, functionally identified neurones; values from fourteen visceral vasoconstrictor neurones shaded (this includes the four visceral vasoconstrictor neurones that had some functional properties of motility-regulating neurones); sixty-seven motility-regulating neurones. *B*, all neurones with resting activity including those without reflex activity ($n = 104$). *C*, resting activity after decentralization of the IMG (cutting all lumbar splanchnic nerves and the intermesenteric nerve); $n = 22$.

modulation with respect to the ECG or to the respiratory cycle. Thus these neurones were not likely to have been visceral vasoconstrictor neurones. The rest of the neurones were silent. Sixteen of these forty-two neurones exhibited weak reflexes on stimulation of the anal mucosa (all of them showing no after-discharges) but could not be classified further because they were lost.

On-going activity

The average rate of on-going activity was determined for 104 postganglionic neurones. The time period over which activity was analysed was 3–10 min and was about 10–20 min after the last afferent stimulus. Figure 8*A* and *B* illustrates the distribution of the rate of on-going activity. The rate of on-going activity in the motility-regulating neurones was $0{\cdot}7 \pm 0{\cdot}5$ impulses s^{-1} (mean $\pm$ S.D., $n = 67$) and ranged from about 0·1 to 2·6 impulses s^{-1}. In the neurones without reflexes the rate of on-going activity was $0{\cdot}6 \pm 0{\cdot}5$ impulses s^{-1} ($n = 23$) and ranged from about 0·1 to 2 impulses s^{-1} with a median of about 0·5 impulses s^{-1}.

There was statistically no difference in the rate of on-going activity between the postganglionic neurones that projected in the ipsilateral (left) HGN (left lumbar splanchnic nerves intact, see Methods) and those that projected in the contralateral (right) HGN (right preganglionic input interrupted, about 20% of the preganglionic input from left side intact; see Baron *et al.* 1986*a*). Therefore the data from both populations of postganglionic neurones were put together.

We did not try to work out the percentages of the postganglionic neurones that were silent and projected into the ipsilateral (left) HGN (ipsilateral lumbar splanchnic nerves intact). Yet it appeared to us that most postganglionic neurones had some on-going activity.

The intervals of the on-going discharges in most neurones exhibited a skewed or a more complex distribution. Six neurones with on-going activity showed very regular discharges. Figure 9 illustrates an experiment in which the activity of two neurones was recorded simultaneously (Fig. 9*A*). Both neurones were activated by electrical stimulation of one of the white rami L3 and L4 with single pulses (see insets in Fig. 9*B* and *C*). The regularity of the on-going discharges is illustrated by the almost normal distribution of the intervals around means of about 0·55 and 0·75 s (Fig. 9*B* and *C*). Two of these neurones were postganglionic type 2 motility-regulating neurones. The other neurones did not appear to be modulated by any of the stimuli tested.

On-going activity after decentralization

In six animals the IMG was completely decentralized towards the end of the experiment by cutting the remaining ipsilateral lumbar splanchnic nerves. Cutting the HGNs and the lumbar colonic nerves had no effect on the level of on-going activity in multi-unit bundles after decentralization. After decentralization, the rate of on-going activity was determined in twenty-two postganglionic neurones that projected in the HGN. Figure 8*B* and *C* compares the distribution of the rate of on-going activity of the neurones before decentralization (*B*) with that after decentralization (*C*). The rate of on-going activity was $0{\cdot}09 \pm 0{\cdot}1$ impulses s^{-1} ($n = 22$) and ranged from 0·01 to 0·3 impulses s^{-1} with a median of about 0·08 impulses s^{-1}, after decentralization.

The percentage of postganglionic neurones with on-going activity after decentralization of the IMG was estimated from the numbers of postganglionic axons in the bundles that were isolated from the HGNs and activated on electrical stimulation of the lumbar splanchnic nerves with single pulses. In this way the frequency of units

with on-going activity was likely to be overestimated. Using this procedure, we estimated that $\leqslant 4\%$ of the postganglionic neurones that project in the HGNs have on-going activity after decentralization *in vivo*. Taking the rates of on-going activity (Fig. 8) and the estimations of the fractions of postganglionic neurones with on-going

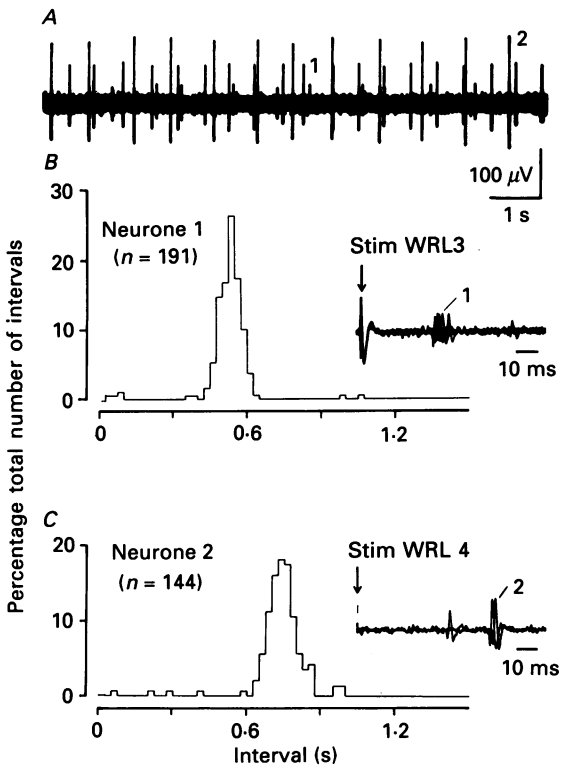

Fig. 9. Two postganglionic neurones with regular on-going activity. *B* and *C*, interval histogram at a bin width of 25 ms (ordinate scale, frequency of intervals per 25 ms). Inset records, activation of the neurones by stimulation of the white rami (WR) L3 and L4 with single pulses (5 V, 0·2 ms pulse duration). Both neurones had a reflex pattern of motility-regulating type 2 neurones.

activity together, we conclude that the overall on-going impulse traffic from the IMG to the pelvic organs decreases to about 1% or less after decentralization.

Segmental origin of the preganglionic synaptic input

The preganglionic inputs were tested by electrical stimulation of the white rami L3 and L4 with single pulses. Most visceral vasoconstrictor neurones (twelve of fourteen neurones) were activated from one of the white rami, but not from both (Fig. 10*A*), whereas the other two groups of neurones were either activated from one of the two white rami (about 50% of the neurones) or from both white rami (Fig. 10*B* and *C*). The difference between the visceral vasoconstrictor neurones and the other postganglionic neurones is not significant (χ^2 test, $P > 0{\cdot}05$). Some neurones (twelve

motility-regulating neurones and five neurones without reflex activity but with on-going activity) could not be activated by either of the two remaining white rami or when both white rami were stimulated together. It is likely that a further white ramus of one of these two segments was missed. In about 50% of cases one segment has two white rami on one side (Baron *et al.* 1985).

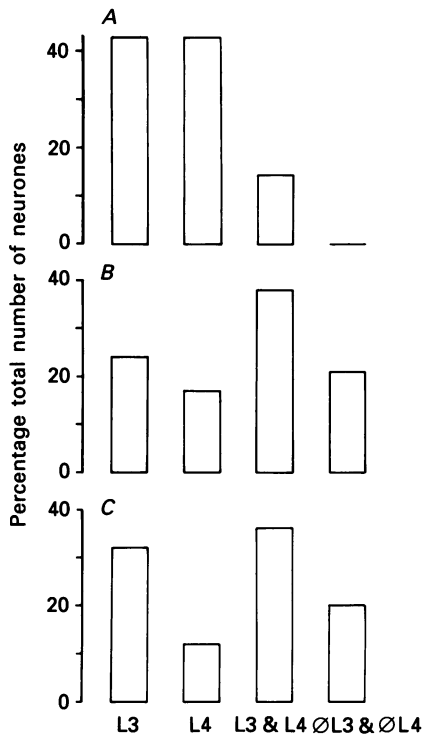

Fig. 10. Segmental origin of preganglionic input (stimulated electrically) to postganglionic neurones. L3, L4: only from white ramus L3 or L4 activated. L3 & L4: activated from both white rami. ∅L3 & ∅L4: neither activated by either white ramus nor when both rami were stimulated together. *A*, visceral vasoconstrictor neurones ($n = 14$); *B*, motility-regulating neurones ($n = 58$); *C*, neurones without reflex activity ($n = 25$).

Preganglionic neurones

About 1300 of the 2300 sympathetic preganglionic neurones that project in the lumbar splanchnic nerves on one side project further in the HGNs (80% in the ipsilateral HGN and 20% in the contralateral HGN). We identified nine preganglionic neurones by their constant latency response to electrical stimulation of one of the white rami and by their on-going and/or reflex activity. Eight neurones had resting activity (mean 0·7 impulses s^{-1}) and one neurone was silent. Two of these neurones behaved like visceral vasoconstrictor neurones, four like motility-regulating neurones, two neurones exhibited no reflexes and one neurone was not tested. Five neurones projected in the white ramus L4 and four in the white ramus L3. The axons of the preganglionic neurones conducted at $2{\cdot}4 \pm 1{\cdot}1$ m s^{-1} (mean $\pm$ S.D., $n = 9$).

DISCUSSION

Table 1 summarizes the results described in this paper. The sympathetic postganglionic neurones projecting in the HGNs can be classed into three groups of functionally different types of neurones: neurones with properties of visceral vasoconstrictor neurones, neurones with properties of motility-regulating neurones, and neurones which exhibited no reflexes. Most of the functionally identified neurones exhibited on-going activity and about 50% of the neurones without reflex activity were spontaneously active. The postganglionic visceral vasoconstrictor neurones are probably associated with the regulation of resistance of the vasculature, the motility-regulating neurones with the regulation of the motility of the lower urinary tract and hindgut (including the internal anal sphincter), and at least some of the silent neurones with the regulation of the internal reproductive organs. The percentages of the different types of postganglionic neurones are remarkably similar to the corresponding percentages that have been described recently for the population of lumbar preganglionic neurones projecting to the IMG (see Table 1, χ^2 test, $P > 0{\cdot}05$; Bahr *et al.* 1986*c*; Jänig & McLachlan, 1987). These similarities in the functional types of neurones and in the frequency of occurrence of the different functional types strongly suggest that the centrally generated impulse activity is reliably transmitted in separate peripheral pathways to the target organs in the pelvic cavity. This separation of sympathetic pathways does not preclude a modulation of the centrally generated messages by events in the IMG.

The functional types of postganglionic neurone worked out in this study, i.e. motility-regulating and visceral vasoconstrictor neurones, may match up with groupings of neurones in the IMG made on the basis of their electrophysiological properties by Cassel, Clark & McLachlan (1986). They found that in the guinea-pig 87% of these neurones fire continuously during prolonged intracellular depolarizing pulses ('tonic' neurones), and the remaining neurones discharge transiently to this stimulus ('phasic' neurones). The latter neurones are identical in their biophysical properties to most paravertebral sympathetic neurones. These different discharge properties largely result from differences in the presence of voltage-sensitive potassium channels in the membrane of the neurones in the guinea-pig IMG. It is tempting to assume – as proposed by the authors – that 'tonic' neurones regulate non-vascular functions and correspond to our motility-regulating neurones and 'phasic' neurones regulate the vasculature and correspond to our visceral vasoconstrictor neurones.

The activity in the postganglionic visceral vasoconstrictor neurones is largely influenced from the arterial baro- and chemoreceptors and relatively little from the visceral receptors. The activity in these neurones is also centrally coupled to the regulation of respiration (Boczek-Funcke *et al.* 1989). There is an overlap in the functional properties between visceral vasoconstrictor and motility-regulating neurones in a small subpopulation (about 20%) of the visceral vasoconstrictor neurones, as has also been described for the lumbar preganglionic visceral vasoconstrictor neurones (Bahr *et al.* 1986*b*). In both the pre- and postganglionic visceral vasoconstrictor/motility-regulating subpopulations the visceral vasoconstrictor properties dominated the pattern and it is possible that discrimination of

TABLE 1. Summary of the experimental results

Neurone type: (1)	Visceral vasoconstrictor (2)	Visceral vasocon/ motil regul[a] (3)	Motility regulating type 1 (4)	Motility regulating type 2 (5)	Motility regulating anal (6)	Unclear[b] (7)
On-going activity	All	All	Most	Most	Most	50%
Rate (impulses s^{-1})[c]	$1{\cdot}1 \pm 1{\cdot}1$		$0{\cdot}7 \pm 0{\cdot}5$	$0{\cdot}7 \pm 0{\cdot}5$	$0{\cdot}6 \pm 0{\cdot}5$	$0{\cdot}6 \pm 0{\cdot}5$
(n)	(14)		(36)	(18)	(7)	(23)
Reflexes from[d]:						
Baroreceptors	Decrease, CR[e]	Decrease, CR	No effect	No effect	No effect	No effect
Chemoreceptors	Increase	Increase	No effect	No effect	No effect	No effect
Urinary bladder	No effect	Increase[f]	Increase	Decrease	No effect	No effect
Colon	No effect		Decrease, no effect	Increase, no effect	No effect	No effect
Anal mucosa	No effect		Increase, some decrease	Increase, some decrease	Increase	No effect
Percentage:						
Postganglionic ($n = 150$)	13	3	34	14	8	28
Preganglionic[g] ($n = 192$)	22	4	33[h]	17	7	17
Proposed target organs	Blood vessels		Urinary bladder, distal colon, internal anal sphincter			Reproductive organs

[a] Visceral vasoconstrictor neurones that have also some functional properties of motility-regulating neurones.
[b] A third of these neurones responded to anal stimulation but could not be analysed further.
[c] Mean ± S.D.
[d] Increase or decrease of activity to stimulation of the receptors/organs listed.
[e] CR, cardiac rhythmicity of the activity.
[f] Activation to stimulation of one of the organs listed.
[g] Data from Bahr *et al.* (1986*c*).
[h] Includes 2% neurones that were excited from both the colon and the urinary bladder.

single units was not perfect in these instances. The percentage of visceral vasoconstrictor neurones is somewhat smaller at the postganglionic site than at the preganglionic one. This may have been just a technical problem or because we cut the lumbar white rami L1 and L2 (see Bahr *et al.* 1986*c*), or alternatively because the pelvic blood vessels may be to a large extent supplied by neurones in the sacral paravertebral ganglia (Langley & Anderson, 1895*c*; Kuo *et al.* 1984).

The reflex activity in the motility-regulating neurones was independent of activity in arterial baroreceptors and chemoreceptors and also independent of the regulation of the respiratory system (Boczek-Funcke *et al.* 1989). Furthermore, motility-regulating neurones were largely responsive to activity in sacral visceral afferents from the pelvic organs. The patterns of reflex activity shown by type 1 and 2 motility-regulating neurones were reciprocally organized. This reciprocal organization of the reflexes also exists for the preganglionic motility-regulating neurones (Bahr *et al.* 1986*a*) and is most likely dependent on the organization of the sacrolumbar pathways in the spinal cord (Bartel *et al.* 1986).

Although stimulation of the afferent input from the anal canal evoked the most powerful reflexes in many motility-regulating neurones, it appeared that (with the exception of the anal motility-regulating neurones) neither type 1 nor type 2 neurones showed any differences in the reflexes elicited by this input (strong or weak reflexes, with and without after-discharges) that allows a subclassification of these neurones. This lack of correlation between the type of reflex elicited by stimulation of the anal canal in motility-regulating neurones with other functional characteristics of the neurones was also found for the population of preganglionic neurones that project to the IMG (Bahr *et al.* 1986*a*; Bartel *et al.* 1986).

Some postganglionic neurones that could not be functionally classified might be associated with the internal reproductive organs. It is reasonable to assume that this applies to those neurones that were completely silent under our experimental conditions, because it is expected that these neurones are only active under special centrally determined conditions. Furthermore it is possible that activity in these neurones is under the control of the hypothalamus and that their central pathways are very sensitive to anaesthesia. The target organs of these neurones would include in males the vas deferentia, the seminal vesicle, the prostate and the proximal urethra. It is also possible that this population of postganglionic neurones contains a subpopulation which when activated vasodilates the helical arteries leading to erection and vasocongestion. Experiments on male cats and dogs (Müller, 1902, 1906; Root & Bard, 1947), as well as observations on male humans (Bors & Comarr, 1960), clearly show that erections can be elicited in adequate behavioural contexts without sacral afferent feedback from the reproductive organs, for example, after destruction of the sacral spinal cord, via the hypogastric pathways. Recent studies by Dail, Walton & Olmstedt (1989) illustrate that even the rat may have this pathway.

From experiments conducted recently on visceral lumbar preganglionic neurones we know that the sacral afferent inflow from the pelvic organs (Bahns *et al.* 1987; Häbler, Jänig & Koltzenburg, 1990; Jänig & Koltzenburg, 1990, 1991) is essential to elicit the reflexes that are typical of motility-regulating neurones. These reflexes were unchanged after cutting the HGNs. Whether lumbar visceral afferents that project

through the HGNs and the lumbar colonic nerves from the lower urinary tract and the colon to the lumbar spinal cord contribute to the reflexes is unknown. These afferents are also excited by contraction and distension of the colon (Blumberg *et al.* 1983; see Jänig & Koltzenburg, 1990) and urinary bladder (Floyd, Hick & Morrison, 1976; Bahns *et al.* 1986). Electrical stimulation of the lumbar afferents elicits weak reflexes in lumbar preganglionic motility-regulating neurones (Bahr *et al.* 1986*c*). Floyd, Hick & Morrison (1982), however, have shown in cats in which the sacral afferents were cut that postganglionic neurones projecting in the HGNs exhibit either excitatory reflexes, inhibitory reflexes, or no reflexes at all to distension of both the urinary bladder and the colon. These results argue that excitation of lumbar visceral afferents may indeed contribute to the reflexes in the motility-regulating neurones and that the reflex patterns may be different from those described in the present study. It must, however, be kept in mind that Morrison and co-workers had additionally cut the buffer nerves containing the afferents from the arterial baroreceptors. They could therefore not differentiate between different types of neurones and it may well be possible that their reflexes occurred in vasoconstrictor neurones. In our previous studies these types of neurones showed considerable reflex activities to electrical stimulation of the lumbar visceral afferents (Bahr *et al.* 1986*c*).

The rate of on-going activity in the postganglionic neurones ranged from about 0·1 to about 2 impulses s^{-1} and was somewhat lower than the rate of on-going activity measured in the preganglionic neurones that project to the IMG (Bahr *et al.* 1986 *c*). This difference is probably real and is unlikely to be explained by our experimental procedure. We eliminated the preganglionic input on one side in order to improve our chances of isolating single postganglionic units from the HGN. Even so, there was no statistically significant difference in the rate of on-going activity in the postganglionic neurones whether or not the preganglionic input was eliminated. On-going activity in the postganglionic neurones was virtually abolished after decentralization of the IMG. In only very few postganglionic neurones (less than 5%) on-going activity of about 0·1 impulses s^{-1} was left. This is consistent with results obtained on ganglionic neurones in the IMG of the cat *in vitro*: in the caudal lobe of the IMG, which contains most of the neurones that project in the HGNs (Baron *et al.* 1986*a*), about 82% of the neurones are silent and 18% of the neurones discharge irregularly (Julé & Szurszewski, 1983). Most of the silent neurones project in the HGNs but only about 10% of the irregularly discharging neurones do, the other neurones projecting through the lumbar colonic nerves to the colon (Julé, Krier & Szurszewski, 1983). The rate of on-going activity measured in our experiments after decentralization is at variance with the rate measured *in vitro* (mean ± S.E.M.: 1·5 ± 0·2 impulses s^{-1} in Julé & Szurszewski, 1983). This discrepancy could be explained if it is proposed that only neurones with a low rate of on-going activity project in the HGNs or that the on-going activity is higher *in vitro* than *in vivo* (blood-perfused ganglion).

It is disappointing, though perhaps interesting, that in this study we were not able to isolate and analyse the responses of many preganglionic neurones projecting in the HGNs. This had been one of the objects of the present study. The neurones we did succeed in isolating and analysing had very slowly conducting axons (even the motility-regulating neurones). There are at least two possible reasons for this failure.

Firstly, it is possible that most preganglionic motility-regulating neurones with fast conducting axons (Bahr *et al.* 1986*c*) do not project in the HGNs or that they project with a slowly conducting branch which is difficult to detect with our dissection technique. If the latter occurs than postganglionic neurones in the inferior mesenteric ganglion which receive synaptic input from preganglionic motility-regulating neurones project in the same HGN as the branches of these motility-regulating neurones. We have found in the completely decentralized preparation (lumbar splanchnic nerves and intermesenteric nerve cut) that electrical stimulation of one HGN elicited only very few impulses in the other HGN in two out of six animals and no responses in the other animals. These responses were blocked by hexamethonium (W. Jänig, M. Schmidt, A. Schnitzler & U. Wesselmann, unpublished observations).

Secondly, it is possible that most lumbar preganglionic neurones projecting in the HGNs are silent and do not exhibit any reflexes to the afferent stimuli we used. If this is the case we would not be able to discriminate between lumbar visceral afferents and the axons of these preganglionic neurones with our electrical identification procedure (see Fig. 1). Thus, it is possible that preganglionic neurones that project in the HGNs comprise a functionally distinct class of neurones that is largely silent.

We conclude that sympathetic postganglionic neurones projecting in the HGNs consist of several functionally distinct types. Neurones that are under predominant control of the arterial baro- and chemoreceptors (visceral vasoconstrictor neurones) may regulate the vasculature of the pelvic organs. Neurones which lack this control and exhibit reflexes to stimulation of sacral visceral afferents from pelvic organs (motility-regulating neurones) may be involved in the regulation of these organs. Though direct evidence is missing we believe that motility-regulating type 1 neurones (excited from the urinary bladder and inhibited or not influenced from the colon) are associated with the distal hindgut and motility-regulating type 2 neurones (which have a reflex pattern opposite to the type 1 neurones) are associated with the lower urinary tract. Finally, silent neurones without reflex activity may be associated with the internal reproductive organs. The study supports the idea that the centrally generated patterns of activity are transmitted from the spinal cord to the target organs in the pelvic cavity in separate pathways (for discussion see Jänig & McLachlan, 1987).

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